HOME RANGE AND ASSOCIATED SOCIOBIOLOGY AND ECOLOGY OF MALE GOLDEN BOWERBIRDS *PRIONODURA NEWTONIANA* (PTILONORHYNCHIDAE)

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Home range and social interactions of male Golden Bowerbirds, *Prionodura newtoniana*, during display seasons and other months of the year, prior to and during bower ownership, were studied for six years (1978-1984) in upland rainforest. Display season was late August to December, the wet season rains terminating activity at bowers. A brief period of post-moult activity occurred in late March to early May. A traditional bower owner never occupied more than one traditional bower site simultaneously or consecutively. Traditional bower sites were usually attended by traditional (>2 seasons) bower owners. In a few instances (n = 3) the disappearance of a long-term traditional site owner resulted in it being temporarily visited for a season(s) by immature males, until one became established as its new owner. Similarly, a rudimentary bower site (n = 4) was established near (50-150m) a traditional site if the latter lost its long-term owner. The rudimentary site was then irregularly attended by immature males, until one became the new owner of the adjacent traditional site.
Young bowerless males actively attended bower sites during peak display season (38% of sightings of them) and during the post-peak display season of March to early May (45% of sightings). From five to two years before attaining traditional bower ownership, immature males visited many bower sites, at an average distance of 391m from the one they eventually came to occupy. The year before attaining full bower site occupancy this distance diminished, to an average 186m, as older immature-plumaged birds focused their activities nearer the site they would eventually occupy. Most males were adult-plumaged by the time they came to actively occupy a traditional site full time, but a few were in immature/sub-adult plumage.
Traditional owners left bowers to forage, bathe, drink, and collect sticks and decorations. They foraged relatively close (mean = 110m) to their bowers, overlapping foraging ranges of neighbouring rival males on occasion. They visited other bowers (mean distance = 191m), mostly (82%) during the display season, to steal decorations. The mean distance travelled from bower sites for all purposes averaged 143m, with a median of 121m (n = 152). Estimated mean home range size of eight adult males was 7ha (range 3-10ha). ❒ *Golden Bowerbird, Prionodura newtoniana, Ptilonorhynchidae, home ranges, bower acquisition, social interactions.*

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Interest in bowerbirds (Ptilonorhynchidae) has seen a recent revival, due to their significance to studies of the evolution of social systems and sexual selection theory (Donaghey, 1981; Pruett-Jones & Pruett-Jones, 1982, 1983; Borgia, 1986; Frith & Frith 1993, 1995; Lenz 1993). Bower structures and building behaviour of male bowerbirds provide opportunities to examine the evolution of symbolic, externalised, secondary sexual characters (Frith & Frith, 1993, 1999a; Borgia, 1995), the evolution of culturally transmitted traits (Diamond, 1986a) and origins of aesthetic sense in animals (Diamond, 1982, 1986b). In view of almost no knowledge of its biology and the potential significance to theoretical considerations of animal social organisations and mating systems in general, and to the evolution of same in bowerbirds particularly, we began studying Golden Bowerbirds *Prionodura newtoniana*, in 1978.

We examined 60 traditional bower sites, involving a total of 98 main (decorated) bower structures, during 1978-1997 on the Paluma Range, and presented a comparative and quantified review of them (Frith & Frith, 2000a). A traditional bower was a large, well-established, structure built at a traditional site that was regularly attended, maintained and decorated throughout subsequent seasons by its traditional adult male owner. We also described short-term, rudimentary, bowers built by immature males at bower sites established near to traditional ones

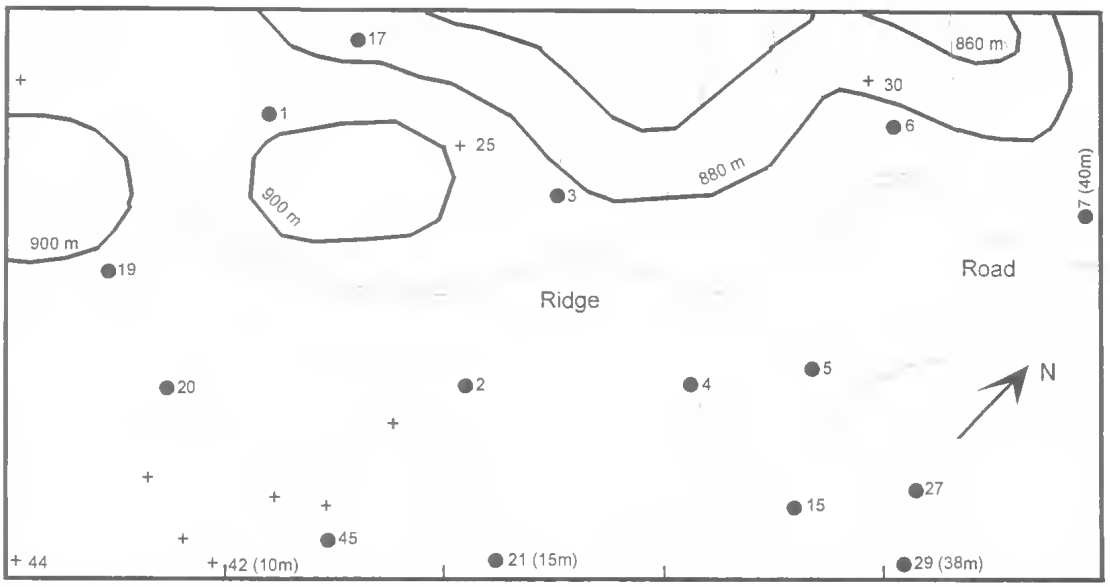

FIG. 1. Dispersion of 15 (including 3 just outside) traditional (●) and 10 (including one on the perimeter) rudimentary (+) male Golden Bowerbird bower sites within 50ha (1 × 0.5km) study area 1 (SA1). Only rudimentary sites at which marked individual birds were sighted are numbered. Faint lines indicate seasonal drainage gullies. Grid marks are indicated at each 200m within the 1km southern boundry on the figure. Bower sites just on/outside the perimeter of SA1 are plotted within the boundary line and their actual distances outside it indicated.

(Frith & Frith, 2000a), a scenario observed in other bowerbirds (Vellenga, 1970, 1980; Donaghey, 1981; Pruett-Jones & Pruett-Jones, 1982; Chaffer, 1984; Borgia, 1986; Lenz, 1993; Frith & Frith, 1994, 1995, 1999a; Frith et al, 1996).

During the display season (late August-December), bower-owning males perch above their bowers and give loud advertisement song and other vocalisations including fine vocal avian mimicry, maintain and decorate their bowers, evict rival males and display to potential mates (Frith & Frith, 2000b). Advertisement song consists of a prolonged, pulsating *rattle*. Other calls include *squeals*, *screeches*, *wolf-whistles*, *scolds*, frog- and cicada-like notes, given as single notes, or as a medley together with fine vocal avian mimicry of >22 model species. Males leave their bower site to harvest sticks and decorations, and steal decorations from rival males for their bower, and to bathe and forage (Frith & Frith, 2000b). They are predominantly frugivorous but also eat beetles, cicadas, and spiders (Frith, 1989; Donaghey, 1996; Frith & Frith, unpubl. data). Availability of fruits, in both time and space, may affect profoundly the home ranges of bowerbirds, but data detailing home ranges of fixed-point courting promiscuous male frugivorous bowerbirds are available only for the Satin, *Ptilonorhynchus violaceus* (Donaghey, 1981), Macgregor's (Pruett-Jones & Pruett-Jones, 1983) and Tooth-billed, *Scenopoeetes dentirostris* (Frith et al., 1994) bowerbirds.

The present study provides the first information on distances travelled by traditional bower-owning male Golden Bowerbirds away from their bower sites. It also describes for the first time activities of immature males prior to becoming the owners of traditional bowers. Seasonal activities at, and away from, bowers during different times of the year are discussed. Data on male attendance levels and their time-budgeted activities at bowers are presented elsewhere (Frith & Frith, 2000b). Results of long-term studies of male survival, histories of bower ownership by individual males, and acquisition of adult plumage will appear elsewhere.

METHODS

STUDY AREA. This study was carried out in upland rainforest, at about 850m asl, on the Paluma Range, 7km from Paluma Township and 80km north of Townsville, northeastern Queensland. The study area (19°00'S, 146°10'E) was a 50h plot, 1 × 0.5km, permanently gridded

with metal stakes (Fig. 1). For a detailed description of this area, see Frith & Frith (2000a). The present study deals mostly with the ownership and movements of male Golden Bowerbirds based at 15 traditional and 4 rudimentary bower sites within, or just outside the perimeter of our study area (Fig. 1). In a few instances, however, birds marked as immature males and resighted within our study area eventually took up ownership of traditional bower sites (n = 6) beyond it. For the location of these bower sites (numbers 16, 22, 23, 24, 33 & 34) see Frith & Frith (2000a: fig. 2).

DEFINITIONS. Definitions of bower sites and structures appear in Frith & Frith (2000a), and of the display season and vocalisations in Frith & Frith (2000b). We refer to a display season by the year in which it started (S78, S79 etc). An immature male was one in female-plumage and a sub-adult male one with some to almost complete adult male plumage intruding into female plumage. We use 'regularly attended' to imply full-time seasonal attendance by traditional owners at traditional bowers, and 'irregularly attended' to imply part-time seasonal attendance by immature males at traditional or rudimentary bowers. All statements refer to males unless stated otherwise.

HOME RANGES. Movements of individually marked males were examined over six display seasons (S78-S84) and additional months of the year. Intensive fieldwork was from 1 August 1978 to 28 February 1981, save 1 May to 18 July 1979 when we were absent (but relative bird activity at bowers was then assessed by Andreé Griffin). In studying Golden and other bowerbird species during this period, 1547 hours were spent carrying out systematic work: 788h during four hour random walks, 572h during fixed transect walks, and 187h of random searching for nests (see Frith, 1984; Frith & Frith 1994, 1995, 1998). Of the total 1547h, 893h were during display season months August-December; 282h during January-February when it was excessively wet and/or males were moulting (Frith & Frith, unpubl. data); 268h during March-May when there was some post-moult activity at bowers; and 104h during winter months June-July. We also spent 343h mist-netting at bowers, as well as marking/retrapping individuals elsewhere during a standardised avifaunal netting programme (Frith & Frith, unpubl. data).

Fieldwork continued through the display season months of S81-S84, and non-display season months of June 1981, February, May and August 1982, June 1983 and March 1984. During S82 and S83 we made observations at six bower sites in September-November 1982 for 369h, and November-December 1983 for 102h. Sightings of marked birds at bowers are presented here, but levels of attendance at bowers and time-budgeted activities at them appear elsewhere (Frith & Frith, 2000b). We continued netting at bower sites and for a general avifaunal netting programme during S81-S84.

Each captured bird was metal banded and with a unique two colour band combination (= marked). Biometrical, morphological and moult data will appear elsewhere (Frith & Frith, unpubl. data). Band colours on bower-owning birds were confirmed each season by direct observation at bowers, to avoid disturbance by retrapping, although many birds were retrapped opportunistically away from bowers. Band colours were also noted during bird sightings at and away from bowers during other fieldwork. The present study deals with 26 confirmed males, first marked during S78-S81 in adult (n = 11) or immature (n = 15) plumage. Numbers of sightings of marked individuals at bower sites were totalled for the months of August-December, January-February, April-May and May-July (S78-S84), in view of the above.

RESULTS

BOWER SITES AND EXISTING OCCUPANCY. *Traditional Bower Sites with Traditional Owners.* Fifteen traditional bower sites were monitored during S78-S84: 12 within the study area and 3 (7, 21 and 29) just beyond it (Fig. 1). All save site 21, which was abandoned after 5 seasons, remained active throughout this study. Twelve of the 15 traditional bower sites were regularly attended over different seasons by a total of 20 individual traditional bower owners. An adult never occupied more than one traditional bower site, simultaneously or consecutively.

Traditional Bower Sites Lacking Traditional Owners. Three of the 15 traditional bower sites (5, 15 and 21) lacked traditional owners throughout the study (Fig. 1). The bower at site 5 was a large and traditional one but those at sites 15 and 21 were rudimentary structures. These three bowers sites were irregularly attended by immatures, as follows:

During S78-S84 we made 114 sightings of female-plumaged individuals (43 sightings of 19 marked males, and 71 of unmarked birds whose behaviour indicated they were male) at sites 5, 15 and 21. Most (62%) of the 114 sightings were at

traditional bower site 5, with fewer sightings at the rudimentary bowers of traditional sites 15 (14%) and 21 (24%). These data are biased, however, because we visited site 5 most often, because more consistent activity was to be observed there. During these sightings we observed immature birds giving single call notes (25 times), continuous medley calls with mimicry (33 times), and advertisement song typical of traditional bower-owners, only 9 times. The latter song was only heard during the display season, but other calls, although mostly (57%) heard during August-December, were also given during January-February (19%), March-April (19%) and May-July (5%).

At these traditional sites, young males rearranged bower sticks and/or decorations, or brought in new ones obtained elsewhere. Bowers had few (<10) decorations, in part because neighbouring adult traditional bower-owners stole them (confirmed by five observations of such thefts). Up to four young males often visited such sites together, where they called, displacement-chased each other whilst flicking/fluttering their wings, and sometimes performed brief display postures.

Rudimentary Bower Sites Lacking Traditional Owners. Four rudimentary bower sites were established near to (mean = 104, range 30-150m) traditional bower sites during S78-S84 and were active for one (site 42), two (site 25) or three non-consecutive (sites 30 and 44) seasons. Another rudimentary site (28) was 150m from traditional site 31 (both sites being outside SA1 beyond traditional site 6 — see Figs 4D & 6A). These rudimentary sites were irregularly attended by immatures, but adults visited them occasionally, presumably to steal decorations.

Rudimentary bower sites were usually first established near a traditional site after the disappearance of the latter's owner. For example, the adult owner of traditional site 31 had been badly injured (base of his rear skull bald, torn and bleeding) prior to being seen at his bower on 29 November 1978. The next day we netted and marked him at nearby rudimentary site 28, where we had sighted a sub-adult and two immatures on several previous occasions. We saw this adult male again in April 1979, his head now healed, being chased about his own traditional site by an unmarked immature. We did not see the healed adult again, and in S79 an unmarked adult occupied traditional site 31 and the adjacent rudimentary site was abandoned.

In October 1979 we marked an apparently diseased adult at rudimentary site 42, who may have been the present/previous owner of nearby traditional site 45 (Fig. 1). This bird's plumage was in poor condition and he had a swollen (21.5mm long × 14.6mm diameter) hard fatty 'bag', possibly an infected preen gland, above his central tail feather bases. He was not seen again, and an immature (black/red) took over traditional site 45 during the latter part of S79.

Rudimentary bowers were usually established during the non-display months of March-July, by immatures which had previously limited their activities to the area surrounding the adjacent traditional site. Sometimes two or three immatures temporarily attended such a rudimentary bower site. By the beginning of the following display season (August/September) the immature(s) would challenge the owner of the adjacent traditional site for occupancy, and by late October/early November the victor exclusively occupied it. The rudimentary site was then abandoned.

During S78-S84 we made 30 sightings of female-plumaged individuals (15 subsequently confirmed males and 15 unmarked birds that were probably male) at four rudimentary bowers (sites 25, 30, 42 and 44; see Fig. 1). During these sightings we heard medley calls with mimicry 14 times, and advertisement song only 3 times. We saw adult males at rudimentary sites 5 times, but did not confirm if they visited them to steal decoration.

ACQUISITION OF A TRADITIONAL BOWER SITE. Fifteen males were marked as immatures; 13 were first captured at an average of 317 ± 243m (range 110-900m) from, and two at, the traditional bower site they subsequently came to occupy. Of these 15 individuals, 14 were first captured within the study area: 8 at/near site 5; 2 at site 21; 1 at rudimentary site 44 (sites lacking traditional owners); and 3 at sites 1, 3 and 6 (sites with traditional owners). The initial capture sites of each of these 14 individuals are indicated in Fig. 2. The 15th bird (pink/red) was first captured at a traditional site outside the study area, but subsequently visited bowers within it (see Fig. 3D).

Males in Adult Plumage. Nine of the 15 marked immatures had acquired adult-plumage before first occupying a traditional bower site. The year in which two of these nine became adult was unknown (orange/orange and green/white; see Fig. 2). Six of them were in their first year of adult plumage when acquiring a traditional bower site,

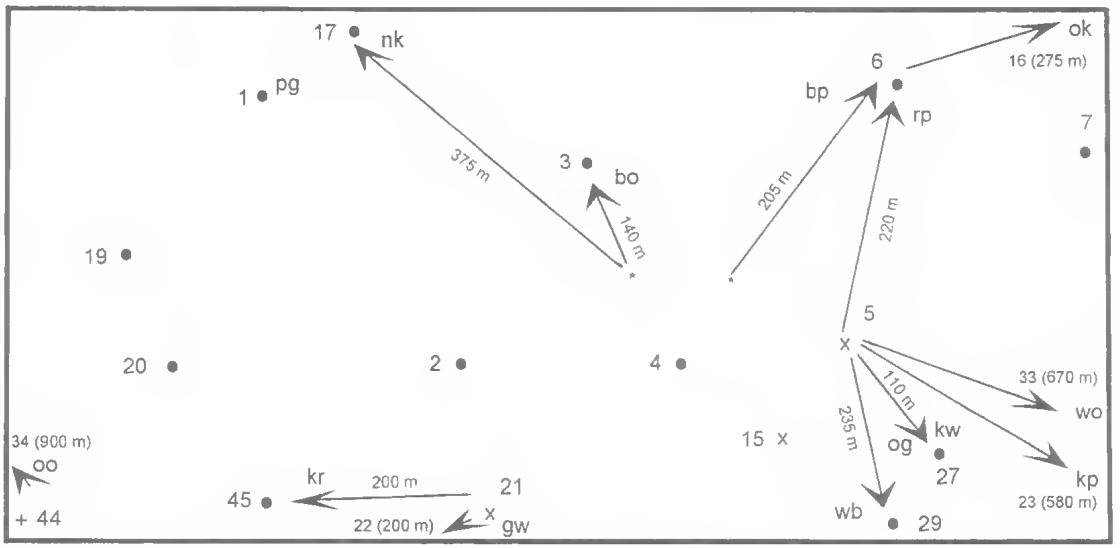

FIG. 2. Schematic plan to scale of localities at which 14 immature male Golden Bowerbirds were captured and marked within study area SA1. The traditional site they subsequently came to occupy and the distance to it from the point of their first capture are indicated. Note: b = blue; g = green; k = black; n = pink; o = orange; p = purple; r = red; w = white; * = capture sites not at bower sites; ● = traditional bower sites with traditional owners; x = traditional bower sites lacking traditional owners; + = rudimentary bower site. Bower sites actually located immediately beyond the SA1 perimeter are here plotted within the boundary line (see Fig. 1 for their distance beyond it).

and another had been adult plumaged for one year, as follows:

Black/white was marked at site 5 in March 1980 as an immature. During March-July 1980 he visited traditional sites with traditional owners, including site 27 (which he later came to own), as well as sites 5 and 15 lacking traditional owners (Fig. 3A). During S80 he was seen at/near site 5 and also at site 6, and its nearby rudimentary bower site 30, while a challenge was underway for ownership of traditional site 6 (see below). Over the next three years (1981-83) we saw him four times, the last being at rudimentary site 30 when he was possibly again challenging for site 6. In August 1984 he was the new owner of traditional site 27, 110m from site 5 where marked 4.5 years previously (Fig. 3A).

White/blue was marked at site 5 in April 79 as an immature. During April 1979-July 80 he visited sites with traditional owners, including site 29 (which he later came to own), as well as sites 5, 15 and 21 lacking traditional owners (Fig. 3B). From August 1980-December 81 he was mostly seen at/near site 5. Early in September 1982, in his first year of adult plumage, he regularly attended site 4 and we assumed he was its new owner, but later that month he was displaced by the owner of the previous season. By September 1983 white/blue was the new owner of traditional site 29, 235m from site 5 where marked 4.5 years previously (Fig. 3B).

White/orange and black/purple were marked at site 5 in March 1980, as immatures. They subsequently took ownership of traditional sites 23 and 33, being 580 and 670m distant from site 5, respectively (Fig. 2). From March 1980 to November 1982 white/orange visited various bowers in the study area but in S84, 4.5 years after marking, he became the new adult-plumaged owner of site 33 (Fig. 3C). Black/purple was re-sighted twice after marking, once in March 1980 at site 27, and again there in January 1981 when in sub-adult plumage and in company of immature white/orange (Fig. 3C). In S82, 2.5 years after marking, black/purple was the adult-plumaged owner of site 23. Another immature, pink/red, was marked in December 1978 at traditional site 24, beyond SA1 but near sites 23 (220m distant) and 33 (165m distant). We saw him six times in SA1 during November 1979 to May 1982, including once with immature white/orange at sites 15 and 27 (Fig. 3D). In S83 he was the new adult owner of site 24, almost five years after being marked there. Thus, the above three males, often sighted together, as immatures, occupied adjacent traditional sites when adults.

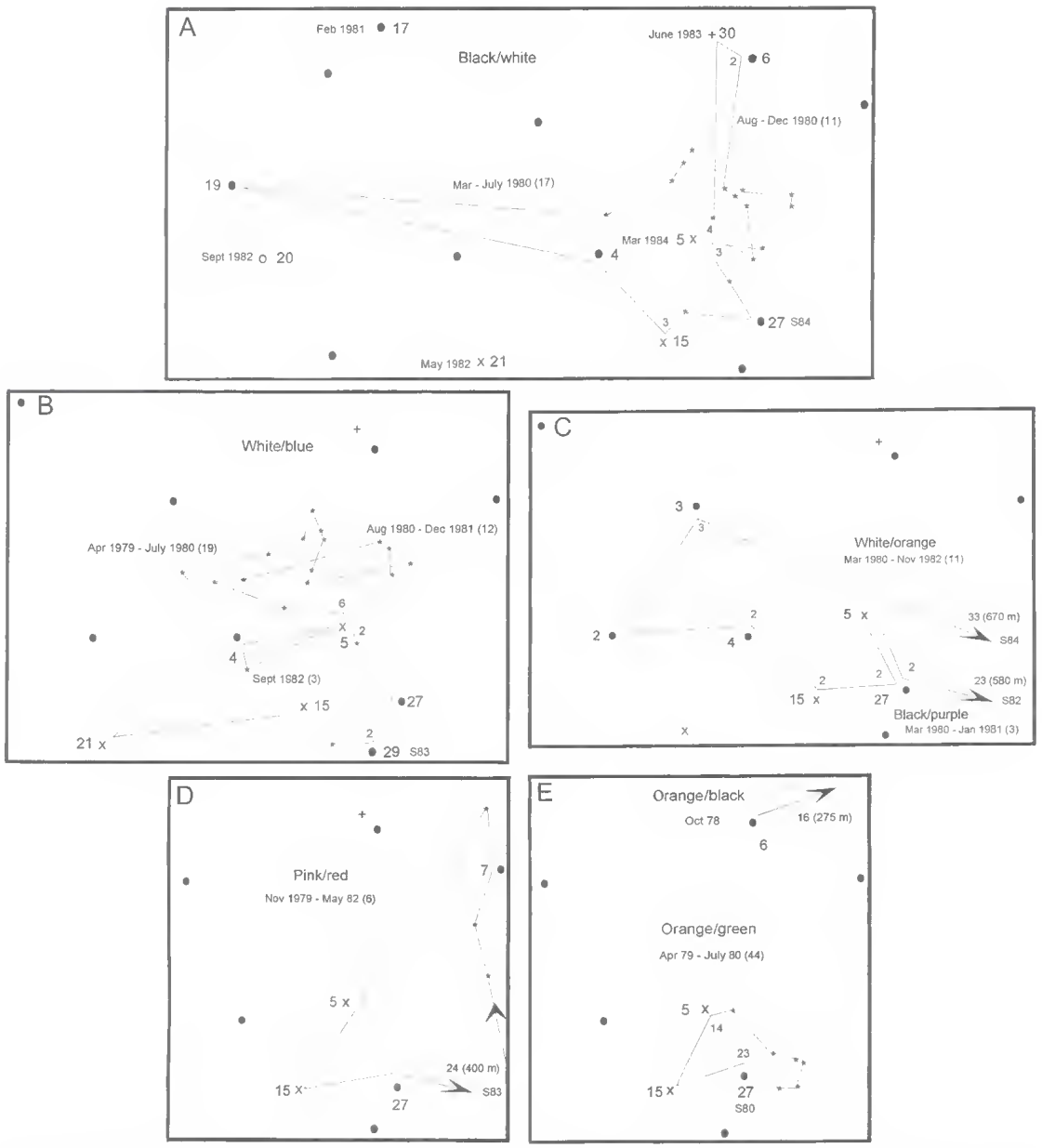

FIG. 3. Schematic plans to scale showing movements of seven immature male Golden Bowerbirds prior to them attaining adult plumage and then acquiring a traditional bower site, during S78-S84 within parts of study area SA1. Number of sightings, months they were made and the season (S) an individual male acquired a traditional bower site are noted within Fig. 3A-E. Bower sites actually located immediately beyond the perimeter are here plotted within the boundary line (see Fig. 1 for their distance beyond it). Distances travelled to bower sites beyond the SA1 boundry are indicated. ● = traditional bower sites with traditional owner; x = traditional bower site lacking traditional owner; and + = rudimentary bower site; * = sightings made other than at bowers.

Two young males took over traditional sites the year after we marked them: orange/black was marked in sub-adult plumage in October 1978 at traditional site 6 and was next seen in S79, as the newly adult-plumaged owner of traditional site 16, 275m from site 6 (see Fig. 3E). Orange/green

was marked at site 5 in April 1979, as an immature. During March-July 1980, having just moulted into adult plumage, he challenged the traditional owner at site 27, being seen there 23 times; including 9 in the traditional owner's presence (Fig. 3E). During August-October of S80 both adults apparently attended site 27. Twice in late October we saw the challenger chasing the owner from the immediate bower area, and in early November he had become the new owner.

Males in Immature Plumage. Six of the 15 marked immatures remained in immature plumage when first occupying a traditional bower site, as follows:

Blue/orange was first marked 230m from bower site 5 in March 1979. From then until July 1980 we sighted him 17 times (see Fig. 4A). During S80 and S81 blue/orange remained closer to bower site 3, which he subsequently came to occupy. By May 1982 blue/orange had built a new bower based upon a pre-existing terrestrial subsidiary structure at site 3, 20m from the old one. He attained adult-plumage in 1983.

Pink/purple, first marked in December 1981 140m from site 3, was seen visiting site 3 and nearby traditionally-owned bowers several times (Fig. 4B). In early September 1982 he regularly attended bower site 1 before being displaced later that month by the owner of the previous season. In S84, still in immature plumage, he was the new owner of site 17. He acquired adult plumage the following year.

During early S78 the bower at traditional site 6 was attended by an adult male, that we marked there on 11 October, but was unseen again after 17 November. Another male, blue/purple, originally marked as an immature 205m from site 6 in January 1979, was seen four times at site 6 during February-March, and once at site 5 in April (Fig. 4C). During the winter months of 1979 a new rudimentary site (site 30) was established, 35m from site 6 (Figs 1 & 4C), and an immature male(s) was attending it but we could not confirm if he was banded. By October immature male blue/purple was the new occupant of site 6, and no more activity was seen at rudimentary site 30 that season. Our last sighting of blue/purple was in May 1979.

Red/purple, first marked in April 1979, started attending rudimentary site 30 together with immature black/white in July 1980, when a challenge was again underway for ownership of traditional site 6 (see above). By late November of S80 red/purple was the established new occupant of site 6 (Fig. 4D). Red/purple may have acquired traditional site 6 early, due to the disappearance of immature-plumaged blue/purple (see above), because he did not become adult-plumaged until 1984, four years after becoming the traditional owner of that site. The bower at rudimentary site 30 was not attended until June 1983, when we saw red/purple (still the owner of site 6) there with black/white. Both birds were now in sub-adult plumage and black/white was possibly again challenging for site 6, but red/purple remained its traditional owner. Rudimentary site 30 was not used again.

Two other immatures had just acquired traditional sites (1 & 45) when first marked. Each site had a derelict bower, which had been abandoned for at least one season. Attendance by these two young males during their first nine months of occupancy was sporadic; as follows:

In March 1979 we found a handful of sticks, 20m from the old bower at site 1 and we marked its immature builder purple/green. In S79, he added little to the new structure, but was seen at rudimentary site 25 (first located by us in S78) and at sites 7, 15 and 27, some 580, 625 and 770m from site 1, respectively (Fig. 5). By S80 he was in adult-plumage and the new traditional owner of site 1. Rudimentary site 25 was abandoned.

In December 1979 we found a small new bower under construction at site 45, 30m from the derelict one. Its builder was immature black/red, who we marked at traditional site 21 (lacking a traditional owner) in October 1979 (Fig. 5). In March 1980 black/red was calling at newly established rudimentary bower site 42, 100m from site 45. By S80 he was the new traditional owner at site 45. Rudimentary site 42 was abandoned. Black/red was sub-adult in S81 and adult plumaged in S82.

HOME RANGES. *Of Non-traditional Bower Owners.* Of 15 immatures, 13 did not own a traditional site when marked and two (purple/green, black/red) were just acquiring one. Three of the 13 bowerless immatures (orange/black, green/blue and green/white) were not sighted after initial capture until adult bower-owners (see Fig. 2). During S78-S84 we made 182 sightings of the remaining 10 individuals: 113 at bower sites and 69 elsewhere (usually foraging; Table 1). Of the 113 sightings at bower sites: 38% were during August-December (courtship season), 5% January-February (wet season), 45% March-May (post-moult activity) and 12% June-July (Table 1).

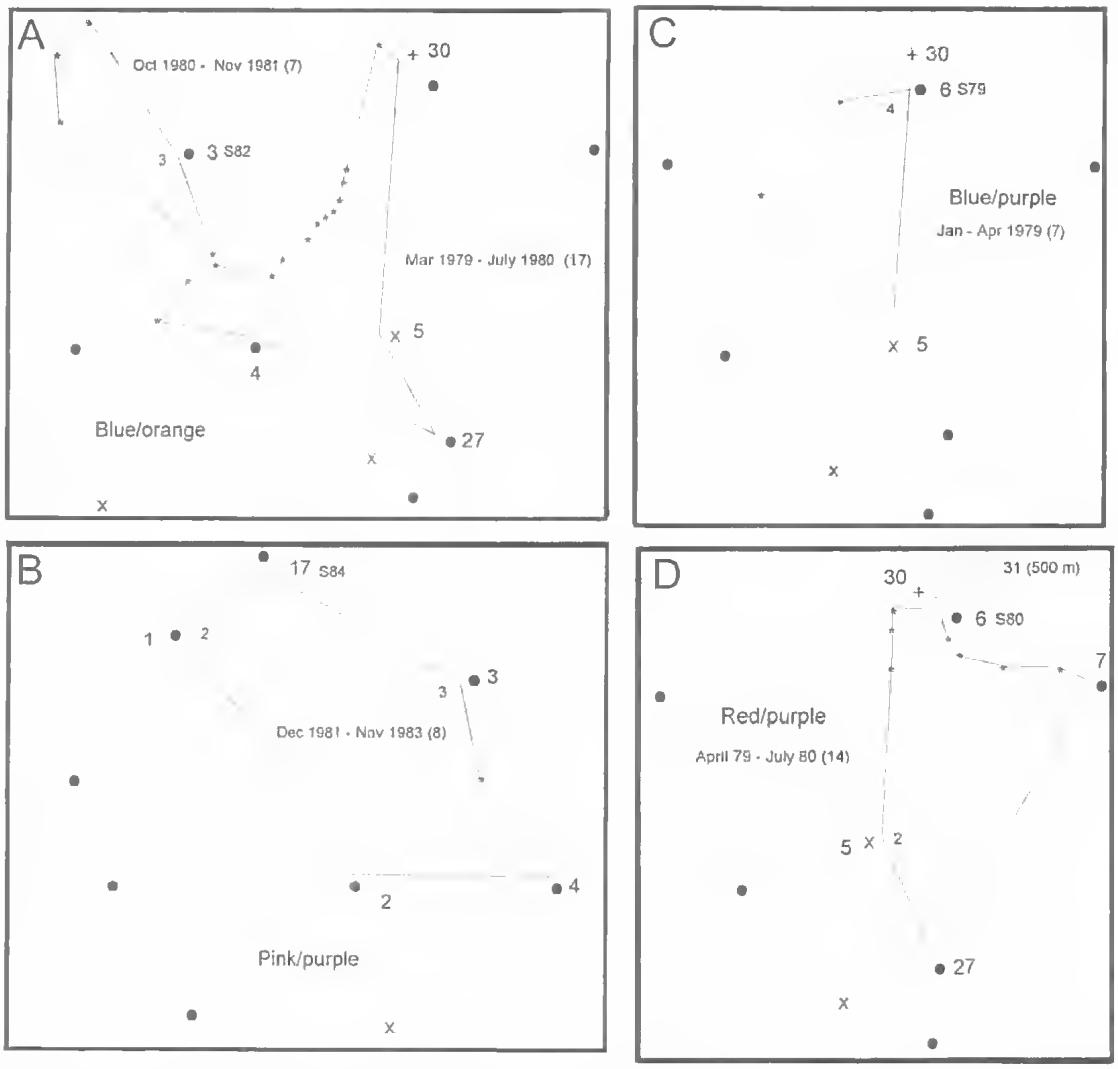

FIG. 4. A-D, Schematic plans to scale showing movements of four immature male Golden Bowerbirds prior to them occupying a traditional bower site while still wearing immature plumage, during S78-S84 within parts of study area SA1. Number of sightings, months they were made, and the season (S) an individual male acquired a traditional bower site are noted. Bower sites actually located immediately beyond the perimeter are here plotted within the boundary line (see Fig. 1 for their distance beyond it). Distances travelled to other bower sites beyond the SA1 boundary are indicated. ● = traditional site with traditional owner; x = traditional bower site lacking traditional owner; and + = rudimentary bower site; * = sightings made other than at bowers.

Of 113 sightings at bower sites: 58% were at traditional sites owned by traditional owners; 39% at sites 5, 15 and 21, lacking traditional owners; and 3% at rudimentary bower sites. These relative proportions varied, however, with individual bird age. Five to two years before the young males owned a traditional site these proportions were 51, 45 and 4%, but one year before such ownership they were 67, 31 and 2%, respectively (see Table 1). These differences reflect the fact that in the year before occupying a traditional site, birds visited it more often, and particularly during March-July (24 of 25 sightings). Between five to two years before establishing bower tenure, immatures visited traditional bower sites more distant (mean = 391m) from their site of future occupancy than they did during the year immediately prior to occupying it (mean = 186m). But sightings of birds away from bowers involved distances

TABLE 1. Histories of sightings of 10 male Golden Bowerbirds marked as immatures (female-plumage) during different periods of months from August 1978-December 1984 at various bower site types and elsewhere. * = only 4 individuals were marked 5 seasons before coming to own a traditional bower site; the other 6 individuals were marked 3 (n = 3), 2 (n = 2) and 1 (n = 1) season before bower occupancy; ** = numbers in parenthesis are sightings of the young males at the bower site of their future occupancy; *** = number of sightings at traditional bower sites 5, 15 and 21 without a traditional owner; **** = 1 sighting represented up to 4 conspecifics visiting a bower simultaneously; see Results.

No. of seasons individuals were marked prior to occupying a traditional bower (no. of individuals *)	Sightings at bower sites						Sightings elsewhere		
	At traditional bower sites		At rudimentary bower sites	At all bower sites	In company of of a conspecific (s) ****	Mean distance (m) from bower site of future occupancy	In total	In company of a conspecific(s) ****	Mean distance (m) from bower site of future occupancy
	with atraditional owner **	lacking a traditional owner ***							
August-December									
5 (n = 4)	2 (1)	0	0	2	0	165	0	0	0
4 (n = 4)	4 (2)	5	0	10	7	400	7	0	80
3 (n = 7)	5	7	0	7	5	230	5	5	315
2 (n = 9)	10 (1)	0	0	11	2	516	0	5	264
1 (n = 10)	5	11	5	16	0	211	10	2	185
Total/mean	**21 (4)**	**10**	1	**13**	**5**	**332**	**23**	**5**	**201**
January-February									
5 (n = 4)	0	0	5	5	0	0	5	0	0
4 (n = 4)	2	0	0	0	2	625	0	0	0
3 (n = 7)	0	0	5	1	0	925	5	0	0
2 (n = 9)	1	5	5	1	5	400	5	5	5
1 (n = 10)	2 (2)	0	5	2	5	5	1	5	205
Total/mean	**6 (2)**	**0**	**5**	**5**	2	**650**	1	**5**	**193**
March-May									
5 (n = 4)	4 (1)	7	5	11	7	356	0	1	166
4 (n = 4)	7	3	5	5	3	400	7	2	325
4 (n = 4)	2	7	5	0	1	356	8	5	166
2 (n = 9)	2	5	1	0	7	250	5	0	202
1 (n = 10)	16 (15)	7	5	20	7	197	7	5	54
Total/mean	**27 (16)**	**23**	**1**	**10**	**10**	**316**	**30**	**3**	**400**
June-July									
5 (n = 4)	0	0	5	0	5	5	7	1	124
4 (n = 4)	1	0	5	0	1	220	5	1	312
3 (n = 7)	5	5	5	5	5	5	0	5	5
2 (n = 9)	**1**	5	0	2	0	255	5	5	5
1 (n = 10)	9 (9)	5	1	11	5	30	0	2	**30**
Total/mean	**11 (9)**	**5**	0	**13**	1	**193**	**10**	7	**165**
August-July									
5 (n = 4)	6 (2)	7	5	**13**	5	344	10	2	142
4 (n = 4)	10 (2)	8	1	19	9	430	19	4	225
3 (n = 7)	3	7	1	10	1	430	13	5	265
2 (n = 9)	14 (1)	7	2	23	9	415	5	2	207
1 (n = 10)	32 (26)	15	1	48	6	186	19	4	123
Total/Mean	**65 (31)**	**44**	**4**	**113**	**30**	**345**	**69**	**15**	**177**

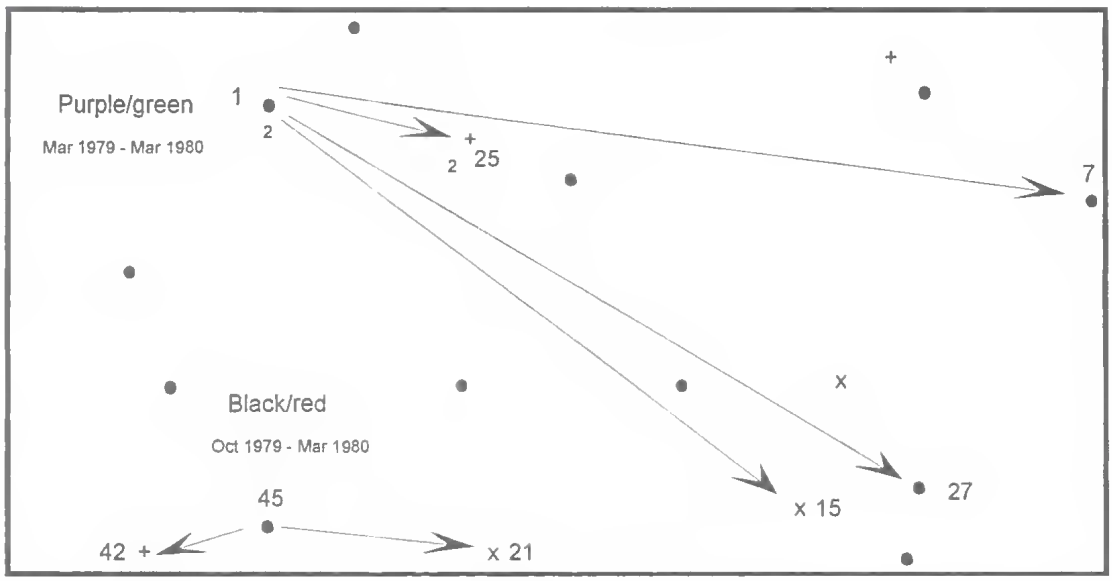

FIG. 5. Schematic plan to scale of the movements of two immature male Golden Bowerbirds that had just occupied a traditional bower site while still wearing immature plumage, during S78-S84 within parts of study area SA1. Number of sightings are indicated. Bower sites actually located immediately beyond the perimeter are here plotted within the boundary line (see Fig. 1 for their distance beyond it). ● = traditional site with traditional owner; x = traditional bower site lacking traditional owner; and + = rudimentary bower site.

closer to the site of their future occupancy, particularly during the season prior to bower ownership (see Table 1).

Of a total of 182 sightings, at bower sites and elsewhere, a marked immature was seen with 1 (n = 29), 2 (n = 8), 3 (n = 7) or 4 (n = 1), marked or unmarked, female-plumaged conspecifics (see Table 1). Twice we saw an immature together with an adult, other than the bower owner, at a bower site. Most sightings (67%) of marked immatures at bower sites 5, 15 and 21 involved two or more individuals, particularly during March-May (63% of sightings).

Of Traditional Bower Owners. During S78-S84 we made 152 sightings of 18 of the total 20 individually marked traditional bower-owners of 12 traditional bower sites in SA1. Sixty-eight were of birds at bower sites neighbouring their own, and 84 elsewhere (Table 2). Of the former 68 sightings: 71% were at traditional sites occupied by a traditional owner; 20% at traditional sites (5, 15 and 21) irregularly attended by immatures; and 9% at rudimentary bower sites attended by young males (Table 2). It is noteworthy that all visits to rudimentary sites were by immatures in their first year of traditional bower-ownership (see *Males in immature plumage*).

Most visitations (82% of 68 sightings) to other bower sites, particularly traditional ones with traditional owners (92%), occurred during display months of late August-December (Table 2). We confirmed that >57% of such visits were to steal decorations (Table 2). Nearly all thefts were from adjacent sites, although a few males travelled further afield to steal (Fig. 6A). Thefts only occurred during the display season.

Distances travelled to other bower sites and elsewhere varied little during different months of the year (summarised in Table 2). Visits by males to bower sites other than their own involved an average distance of 191m (n = 68, range 40-488m) with a median of 195m, and to elsewhere (usually to forage) averaged 110m (n = 84, range 13-300m) with a median of 88m (Table 2). Thus, males remained closer to their traditional sites when foraging (or harvesting a decoration) than in visiting other bowers. Foraging home ranges rarely overlapped those of neighbouring male bower owners (Fig. 6B). Mean distance travelled from bower sites to all localities averaged 144m (n = 152) with a median of 121m. By plotting all sightings of marked owners at eight traditional bower sites (i.e. Fig. 6A and B combined), and drawing polygons based upon the outermost for each (Fig. 6C), we estimated

TABLE 2. Histories of sightings of 18 traditional bower-owning male Golden Bowerbirds at 12 traditional sites during different periods of months from August 1978-December 1984 at bower sites other than their own and elsewhere. * = number of sightings at traditional bower sites 5, 15 and 21 lacking a traditional owner; ** = decoration theft confirmed, but some other sightings probably also involved theft; *** = one sighting was with one conspecific; see Results.

	Sightings at bower sites							Sightings elsewhere		
	At traditional bower sites		At rudimentary bower sites	At all bower sites	For decoration theft **	In company of a conspecific ***	Mean distance (m) travelled to other bower sites	Away from their bower site	In company of a conspecific ***	Mean distance (m) travelled to other bower sites
Months	with a traditional owner	lacking a traditional owner *								
August-December	45	9	2	56	39	1	205	35	4	125
January-February	2	0	0	2	0	0	168	9	0	106
March-May	1	3	3	7	0	1	156	28	1	110
June-July	0	2	1	3	0	2	175	12	0	102
Total/ mean	48	14	6	68	39	4	191	84	5	110

mean overall home range to be 7ha (range 3-10ha).

On nine occasions we saw an adult in the company of an immature, four whilst an adult visited another traditional site, and five times while foraging in the same fruiting tree (Table 2). While bower owning males vigorously displaced, and then chased, rival males out of their bower site, we recorded only one instance of apparent territoriality beyond bower sites. Adult males, from two adjacent bower sites, were aggressively challenging each other along a 200m length of narrow trail in rainforest equidistant between their bower sites. The birds gave scold and other calls, and flicked their wings in agitated fashion, while flying back and forth along their respective sides of, but not across, the trail. On another occasion two adult males foraged in the same fruiting tree without aggression.

DISCUSSION

Most traditional Golden Bowerbird bower sites are occupied by successive generations of adult males (Frith & Frith, 2000a; unpubl. data). Takeovers of traditional sites usually involved an intruding male being in his first year of adult plumage. In a few instances, a traditional bower-owner was not replaced immediately by another adult male and, then, one of three things happened. a) A short-term rudimentary bower site was established close to the vacated traditional site, by immature males building a rudimentary structure there. This was abandoned once one male began regular attendance at the traditional site. b) A vacated traditional bower site was temporarily and irregularly attended by immature males who maintained the existing traditional bower, or built a rudimentary one. Such a new rudimentary bower might subsequently become a larger traditional one, as a new owner regularly attended the site (Frith & Frith, 2000a, unpubl. data). c) But rarely, a traditional site was simply abandoned. Abandoned traditional sites may, however, be re-established during subsequent seasons.

An immature male Golden Bowerbird wanders among the male population for at least five to six years before attaining first signs of adult plumage (Frith & Frith, unpubl. data). This wandering period possibly permits the novice to experience the social/sexual environment, while his female appearance avoids stimulating aggressive responses from adult males. This provides a gradual 'apprenticeship' into the intensely competitive male mating hierarchy, as has also been postulated for males of the sexually dimorphic polygynous manakin (Pipridae) and bird of paradise (Paradisaeidae) species (Lill, 1974a,b; Snow, 1976; Frith & Beehler, 1998). It has been suggested that the long retention of female plumage by males of such species might be part of a mating strategy, involving sexually active males thus concealing their reproductive status (Rohwer et al. 1980, Laska et al., 1992). Immature male Goldens moved extensively about the habitat visiting bower sites, mostly during display months of late August-December, and during the brief period of renewed activity that occurred in late March-

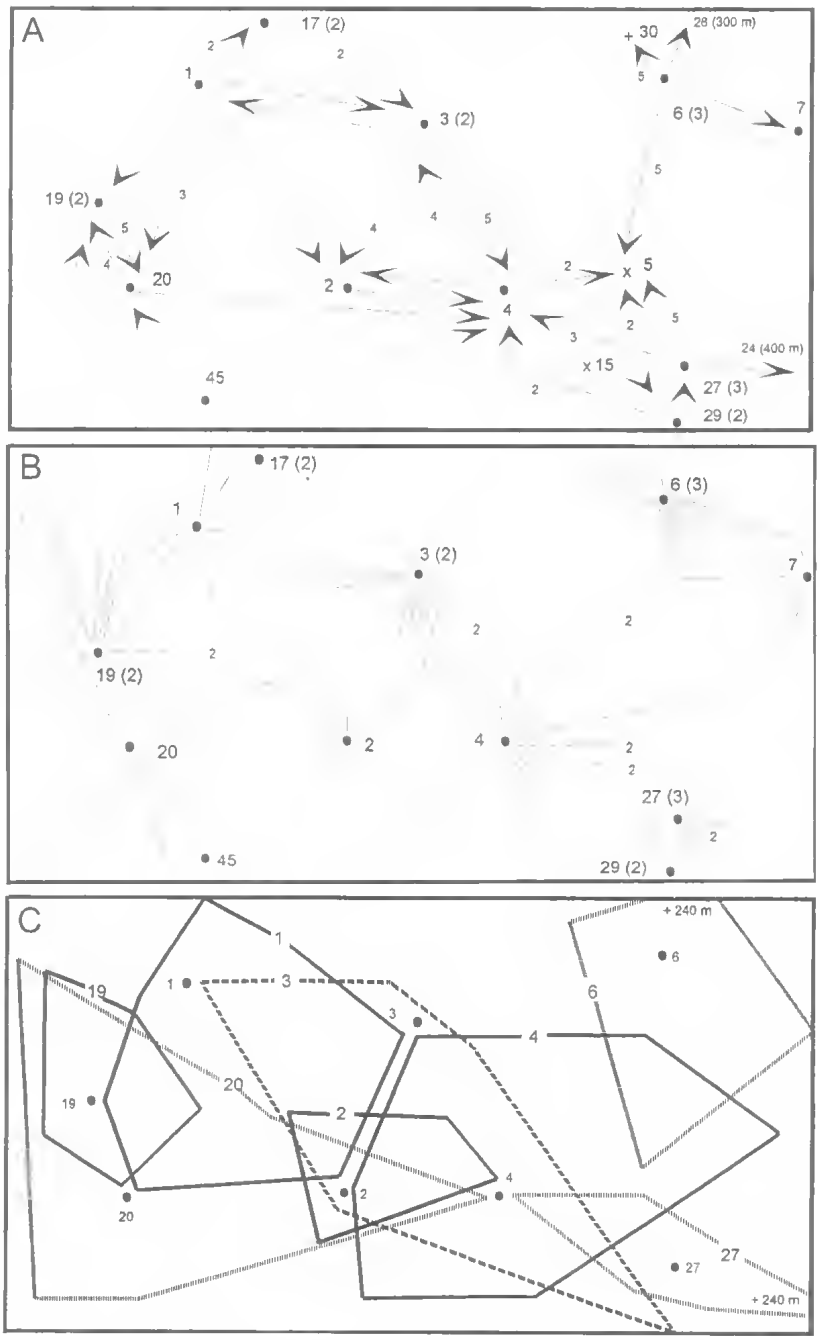

FIG. 6. Schematic plans to scale of the movements of 18 traditional male owners of 12 traditional Golden Bowerbird bowers: A, to neighbouring bower sites; or B, to elsewhere; usually when foraging within part of study area SA1, during S78-S84. C, Approximated home ranges, produced by encompassing all bower visits and sightings elsewhere into polygons. Note: a number in parenthesis after a bower site number indicates the number of consecutive individual traditional owners during this study. Smaller typeface numbers on arrow lines indicate the number of movements/visits. Bower sites actually located immediately beyond the perimeter are here plotted within the boundary line (see Fig. 1 for their distance beyond it). Distances travelled to other bower sites beyond SA1 are indicated. ● = traditional site with traditional owner; x = traditional bower site lacking traditional owner; and + = rudimentary bower site.

early May. Having completed their moult, young males were also notably active at traditional sites during March-early May, when traditional owners were less often in attendance and completing their moult (Frith & Frith, unpubl. data). One year before becoming full-time bower owners themselves, immatures spent more time at traditional sites occupied by traditional owners, especially at the site they were challenging for and subsequently occupied. Such visits increased notably during March-July of the season of subsequent tenure, the challenger having usually just attained adult plumage.

Bower attendance by traditional owners at their own sites was mainly during display and breeding months (Frith & Frith, 1998, 2000b). During this time of year they frequently visited bowers of rival males to steal decorations (Table 2). In recent years bower decoration theft has been studied intensively in other species, and it has been demonstrated that males steal predominantly from immediate neighbours (Borgia, 1985; Pruett-Jones & Pruett-Jones, 1994; Frith & Frith, 1993, 1994, 1995, 2000b). Our observations show Golden Bowerbirds do likewise, as demonstrated in Figure 6. For a discussion on bower decorations and their theft see Frith & Frith (2000b).

Distances traditional bower-owning Golden Bowerbirds travelled from their own bower to other bower sites to steal decorations averaged 191m (median 195m). Distances covered to forage and harvest decorations, were shorter (mean = 110m, median = 88m). The overall median distance males travelled from their bower sites was 121m. This latter figure for male bower-owning Macgregor's Bowerbird was 88m (Pruett-Jones & Pruett-Jones, 1983) and for court-owning Tooth-billed Bowerbirds was 59m (Frith et. al, 1994), despite the latter species travelling longer distances to bathe/drink at creeks (not observed in Golden Bowerbirds by us). Similarly, the median distance of 88m travelled by Goldens to forage is more than double that (32m) observed in Tooth-bills (Frith et al., 1994). These differences may reflect the sparsely and evenly dispersed males/bowers of Macgregor's and Goldens, in contrast with the densely clumped, dispersion of Tooth-bills' courts. It could also indicate the relative abundance of foods of the latter species.

Male Satin Bowerbirds were found to mostly (82%) forage within 50m of their bowers during the breeding season of October-December (Donaghey, 1981). These ate far more insects during this period than at other times (40-50% of their November-December diet). During winter, however, 81% of foraging males were up to 200m from their bowers, and the furthest 350m. Male Satins do not form leks, but disperse bowers linearly along forest edges at a mean inter-bower distance of 312m (Donaghey, 1981) to 500m (Marchant, 1992). The latter author wrote of males thus having 'a territory of about 20 ha'. Vellenga (1980) wrote of each adult male Satin holding a territory that included the rudimentary bowers of (dominated) younger males. Although territoriality beyond the bower site would be less surprising in this more insectivorous bowerbird than in highly frugivorous ones (Beehler & Pruett-Jones, 1983; see below) this requires study and clarification.

We estimated the mean year-round home range of (one or several consecutive) Golden Bowerbird male owners of eight traditional bower sites to be 7ha. Mean home range of four radio-tracked adult male Tooth-billed Bowerbirds was determined to be 9.5ha, although males foraged over a smaller area (Frith et al., 1994). Data available for fixed-point-displaying polygynous and frugivorous species of other passerine groups so studied include the neotropical Manakins, and Cotingas (Cotingidae), (Snow, 1970; Snow, 1962a,b, 1992; Lill, 1974a,b, 1976; McDonald, 1989; Thery, 1990; Prum et al., 1996). These studies found that adult males defend a focal display site, or territory, while foraging over a far more extensive undefended area, or home range. Beehler and Pruett-Jones (1983) reviewed spatial dispersion of adult males in nine polygynous bird of paradise species, in which males are known or presumed to be promiscuous and to court at fixed point display sites (Frith & Beehler, 1998). They related dispersion to diets, and found that males of species with a predominantly arthropod diet were territorial whilst those of predominantly frugivorous ones were not. Obligate insectivores defended exclusive territories, highly frugivorous species formed leks, and species with intermediate diets showed intermediate patterns of dispersion. Thus while males of all species defend their display sites, only those of the more insectivorous species defend a foraging territory while males of more frugivorous ones forage over an undefended home range.

Adult male Golden Bowerbirds vigorously defended their bower site against rivals, but we saw too little of adult males together away from bowers to assess the nature of interactions there.

While male Macgregor's Bowerbirds aggressively defend bower sites, few aggressive interactions occurred away from them (Pruett-Jones & Pruett-Jones, 1982). Our findings suggest the observation that 'Although males do not defend territories in the usual sense, they do occupy areas over which they exert dominance. We do not mean that males exclude rivals from the area (beyond the bower site) or prevent them from foraging there, but that they do prevent rivals from establishing courtship sites' (Beehler & Foster, 1988) is applicable to male Golden Bowerbirds. Further field work is required to clarify the question of (undefended) foraging home range versus the extent of (defended) territory in this species.

Fruit in tropical rainforest is largely economically undefendable by passerine birds, as a result of its spatial and temporal unpredictability (Snow, 1976; Lill, 1976; Beehler, 1983; Beehler & Pruett-Jones, 1983; Frith & Beehler, 1998). Thus the loss of extensive territoriality in predominantly frugivorous species, such as the Golden Bowerbird. Fruit availability in time and space may therefore have profound effects upon home ranges of bowerbirds (Beehler & Pruett-Jones, 1983; Frith et al., 1994). Male bowerbirds must remain close to their bowers if they are to successfully defend their structures and decorations from rivals, and attract and mate females (Frith & Frith, 1993). They attempt to maximise time spent at their bowers, as do Tooth-billed Bowerbirds at their courts (Moore, 1991; Frith & Frith, 1994). This is predictable behaviour for a population of promiscuous males that must compete for opportunities to fertilise numerous females at a fixed focal site during a relatively brief mating season (Frith & Frith, 1993, 1995).

Snow (1976) considered a predominantly frugivorous diet the main pre-condition to a polygynous mating system, in which rainforest dwelling male passerines spend most of their time in advertising/attending/defending a traditional focal courtship area and performing elaborate courtship. Seasonal abundance of fruit in the habitat is theoretically so great as to enable males to be emancipated from nesting duties, and females to nest alone and unaided. In tropical rainforest-dwelling and predominantly frugivorous Golden Bowerbirds, and in many other ecologically similar passerines, the fruit diet would appear to have greatly influenced the evolution of a polygynous mating system, associated morphology, male survival and longevity, dispersion, focal courtship sites with territoriality limited to them, and undefended home ranges (Snow, 1976; Frith & Beehler, 1998).

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